THE

AMERICAN NATURALIST

Vol. XLIII June, 1909 No. 510

HEREDITY AND VARIATION IN THE SIMPLEST ORGANISMS [1]

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UNICELLULAR animals present all the problems of heredity and variation in miniature. The struggle for existence in a fauna of untold thousands showing as much variety of form and function as any higher group, works itself out, with ultimate survival of the fittest, in a few days under our eyes, in a finger bowl. For studying heredity and variation we get a generation a day, and we may keep unlimited numbers of pedigreed stock in a watch glass that can be placed under the microscope.

Work in this field, so far as it has yet been carried, gives in simple form results which are typical of the trend of investigation over the entire subject; it gives a sort of diagram of the main facts of heredity and variation. For this reason it appears worth while to present here the main results in their bearing on general questions. Technical accounts of the investigations have been published elsewhere,[2] but these are rather forbidding, owing

[1] A paper read before the Scientific Association of Johns Hopkins University.

[2] Jennings, H. S., "Heredity, Variation and Evolution in Protozoa." I, "The Fate of New Structural Characters in Paramecium, with Special Reference to the Question of the Inheritance of Acquired Characters in Protozoa," *Journ. Exper. Zool.*, 5, 1908, 577–632. II, "Heredity of Size and Form in Paramecium, with Studies of Growth, Environmental Action and Selection," *Proc. Amer. Philosophical Soc.*, 47, 1909, 393–546.

to the mass of statistical data involved. For the evidence of the statements here made the reader is referred to these.

Unicellular organisms are essentially free germ cells —germ cells that are subjected to the immediate action of the environment, both direct and selective. For long periods they propagate without that intercrossing which so tremendously complicates the study of heredity in higher animals. Here if anywhere we should see readily the effects of environment and of selection in modifying a race.

Let us look first at the direct action of the environment: the "inheritance of acquired characters." It has commonly been thought that under the conditions found in these organisms "acquired characters" are readily inherited. This is because the progeny arise by division of the parents; they are therefore the *same* as the parent. It would seem a matter of course therefore that they should have the same characteristics as the parent, however these characteristics arose.

But when we examine just what occurs in the production of the new individuals, we find—as usually happens when we look closely at biological processes—that the thing is not so simple after all. We find that in reproduction the characteristic features of the parent disappear[3] and are produced anew in the offspring. Thus in Paramecium (Fig. 1) the characteristic form of the ends, the oral groove, the shape of the body—these disappear during fission, and reappear in the growth of the young. In Stylonychia (Fig. 2) all the appendages are absorbed at division; they appear anew in the young, in their characteristic structure, number and distribution, by a process comparable to the development of organs in a higher animal.

[3] Certain exceptions to this, of no theoretical importance, are mentioned in the original papers. Certain characters sometimes pass directly to *one* of the offspring, but their multiplication is of course always by new production.

Reproduction in these creatures may then be compared to the dissolving of a crystal in its mother fluid; on re-crystallization the new crystal appears with the same form and angles as the parent. But it is really a new

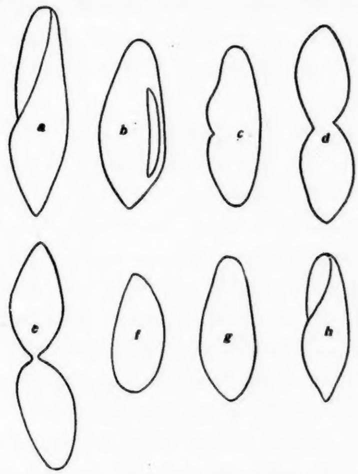

FIG. 1. Changes in form shown by Paramecium during reproduction. *a*, form of adult; *b* to *e*, successive stages of fission; *f*, *g*, immature young; *h*, young after reaching adult form.

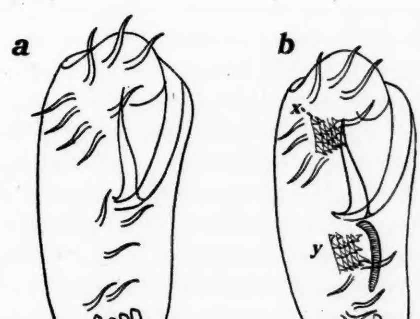

FIG. 2. Stylonychia, after Wallengren. *a*, adult, showing the appendages; *b*, stage preparatory to fission. At *x* and *y* have appeared the beginnings of the new sets of appendages of the two progeny to result from fission, after the disappearance of the old appendages.

crystal, with new-formed angles. The analogy of reproduction with recrystallization is striking in many ways, as we shall see farther.

Thus inheritance is, here as elsewhere, not transmission but new production. The question of heredity then is: What characters will thus be produced anew? Will the progeny reproduce *any* character that the parent happens to have?

When we study the matter in such an organism as Paramecium (Fig. 1), we find that all the characters common to the race—the "normal" characters—are regularly reproduced. But how about characters that are not typical; characters that have been produced in the individual parent by the environment; "abnormal" characters, and the like? It is easy to produce such new characters by environmental action, and it is easy to find in certain cultures individuals that present unusual features. Specimens with altered form, with new appendages, with differently arranged parts, are not very rare. Many of those found in natural cultures correspond in appearance to what we might expect of a *mutation.*

Will such untypical characters reappear in the progeny, so that we shall get a race with the new characteristic?

Examination of a large number of cases in Paramecium shows that these untypical characters are never reproduced in the young. Sometimes such a thing as an appendage may pass bodily to one of the progeny, just as a parasite clinging to the outer surface might do; but there is no multiplication of such a character; no tendency to produce a race bearing it. The young reappear in the form typical for the race, without regard to the individual peculiarities of the parent.[4]

What is produced in the new generation therefore depends on the fundamental constitution of the race, not on the accidental form of the parent. Again the analogy

[4] For many examples of this, with figures, see the first of the papers already referred to.

with crystallization forces itself on us. The characteristic form of crystals is easily changed; by filing off the angles we might convert a large number of pyramidal crystals into the quite new form of cubes. But if we dissolve these and allow them to recrystallize, we obtain, not cubes, like the parents, but the original crystalline form characteristic for that particular chemical compound.

If we should modify the chemical constitution of the substance, it would then crystallize in new shapes. If we could modify the fundamental constitution of the organism we should probably find it likewise appearing in new forms. Whether this occurs at times in unicellular organisms we shall ask later. But it is important to grasp the fact that it does not occur often nor easily; that the ordinary activities of life do not observably bring it about; that the mere presence of a new character in the parent has no evident tendency to produce such a result. Many of the untypical forms found in Paramecium were such as one might imagine due to an alteration in the fundamental constitution of the race (a mutation?), but the new characteristic was not reproduced in the progeny.

But besides the untypical or "abnormal" characters of certain individuals, there are the common differences among individuals that are fully "normal." In the Protozoa, as in all organisms, differences in size and proportion among differing individuals are common; *variation* is the rule here as everywhere. We must then examine these differences, under the question already set forth: What characters are produced anew in reproduction? Will the progeny produce anew these diversities of the parents, in such a way that from large parents arise large progeny, from small parents small progeny, from intermediate parents intermediate progeny?

In Paramecium we find individuals differing greatly in size. From a "wild" lot of Paramecia we isolate such differing individuals and propagate from them, all under

the same conditions. We find that many of these differences *are* inherited; from large individuals we get large races; from small individuals small ones. We find, then, that Paramecium consists of many races, differing from each other in mean size slightly but constantly. Eight of these different races were isolated and propagated for hundreds of generations; some were carried through several complete "life cycles." Each such race consisted of specimens all derived from a single parent individual. Unquestionably many other races exist, that could be isolated by proper means.

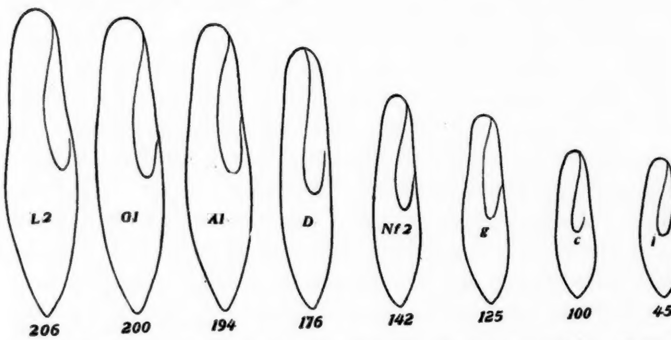

FIG. 3. Diagram showing the relative mean lengths of the eight different races of Paramecium that were isolated. The magnification is about 340 diameters. The actual mean length of each race is given in microns below the corresponding outline.

Fig. 3 is a diagram showing the relative mean lengths of the eight races isolated, as determined by measuring at intervals lots of 100 or more individuals of each race. The mean length for any race is constant under given conditions. The differences between adjacent races are very slight; thus, between the races *c* and *i* of the diagram the difference in mean length was but five to seven microns or .00028 inch. For measuring such constant differences between races even the "fourth decimal place of the biometrician," so heavily contemned of late, would seem to be required. This gives us something of a measure of the minuteness of the steps by which evolu-

tion may occur, if we hold that one of these races has arisen from another.

We find then that by selection we can isolate many races of different mean size, and that the relative mean size is inherited in each race.

But another fact of equal importance comes forth. Within each race (derived from a single parent) the size of the different component individuals varies extremely. The largest specimens of a given race are more than twice as long as the smallest specimens, and every intermediate dimension occurs. We may therefore represent the composition of a single race by the diagram of Fig. 4. These

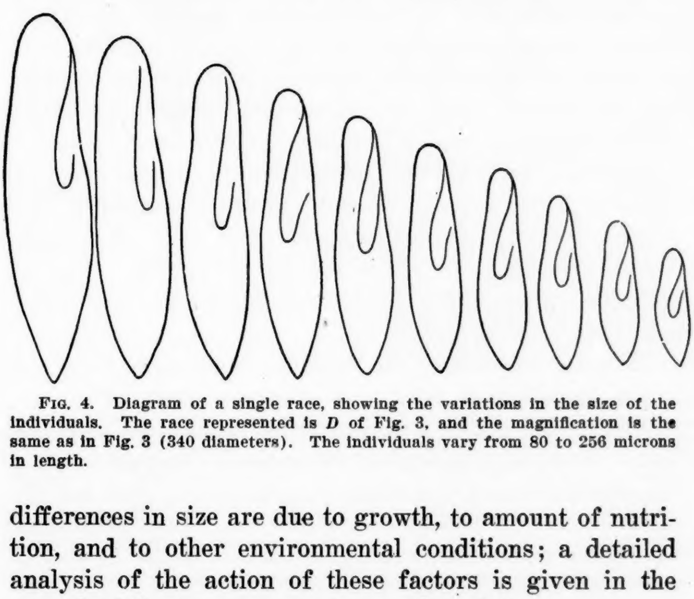

FIG. 4. Diagram of a single race, showing the variations in the size of the individuals. The race represented is *D* of Fig. 3, and the magnification is the same as in Fig. 3 (340 diameters). The individuals vary from 80 to 256 microns in length.

differences in size are due to growth, to amount of nutrition, and to other environmental conditions; a detailed analysis of the action of these factors is given in the second of the two papers above referred to.

Now we come to the most important point. Are the varying sizes within the single race inherited? Will large specimens produce large progeny, small ones small progeny, so that from a single race we can get several, of differing sizes? And can we by repeated selections of

the largest individuals for breeding steadily increase the mean size of a race?

Breeding from the extreme specimens—the largest and smallest—of a single race, we get several hundred individuals from each. *Both produce progeny of the same mean size.* Each produces a whole series of varying individuals, just like the original racial series (Fig. 4); the series produced by the largest individual is exactly like that produced by the smallest, or by any other. The differences between the individuals within such a series are due to growth and environment. Such differences are not inherited: *the race breeds true,* without regard to the peculiarities of the individual parent. A great number of such breeding experiments were carried out, in which selection was continued for many generations, but the results were invariably the same. *Selection within the pure race is of no effect on the size.*

Furthermore, marked differences in the parents due to different environments become quickly equalized in the progeny when the environments are made the same. Thus environmental effects are not inherited. Neither selection nor environmental action changes the size of the pure race.

Thus in our study of the "normal" variations we come to the same result as in our previous study of abnormalities, new characters, apparent mutations, and the like. What is produced in inheritance depends, not on the evident external features of the parent cell, but on the fundamental constitution of the race. Each race has its own peculiar constitution, and under different conditions this same constitution gives rise to various sizes and forms, producing thus the variations within a race, illustrated in Fig. 4. But all these different individuals of a race are potentially the same; at the same age and under the same conditions throughout, all would be alike.

Now consider again the species as a whole: in this

case Paramecium (*aurelia* or *caudatum* or both).[5] We have found it made up in the way indicated in Fig. 5. It consists of a series of many races, differing in mean size; while each race is made up of a series of individuals,

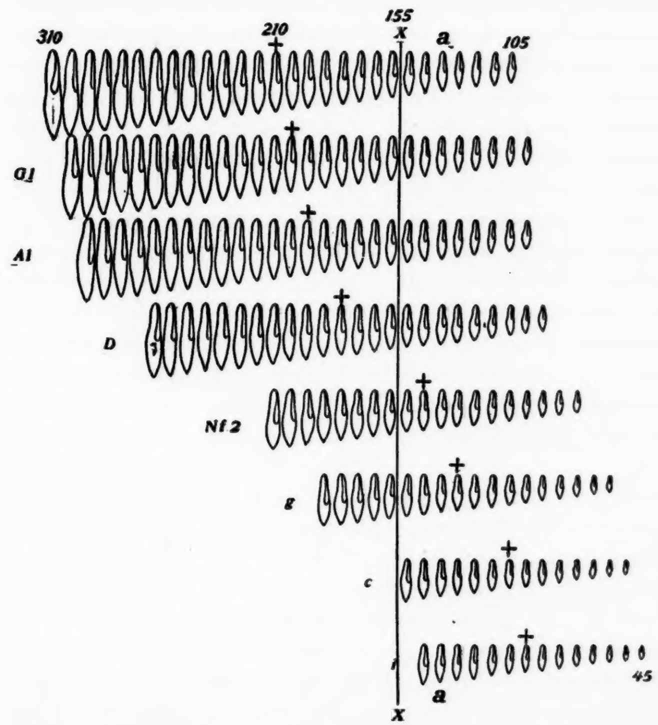

FIG. 5. Diagram of the species of Paramecium, as made up of the eight different races of Fig. 3. Each horizontal row represents a single race. The individual showing the mean size in each race is indicated by a cross placed above it. The mean of the entire lot is shown at *x–x*. The numbers show the measurements in microns. The magnification is about 43 diameters.

that are of varying size, though potentially alike. Reference to this diagram will help to understand certain fundamental facts of variation, heredity and the effects of selection in these organisms.

[5] For a discussion of the species question in Paramecium see the second of the original papers, pp. 498–500.

As the diagram shows, individuals of the same size are found in many different races. An individual of the size shown at *a* might belong to any one of the eight races. Thus from individuals of the same size we may get many different results in breeding. Similarly, individuals of very different size (as the extremes of any horizontal series) may produce progeny of identically the same character. We can not tell by its external characters to what race a specimen belongs; breeding is the only test. In higher organisms, as is well known, we often find a similar state of affairs.

How will selection act on such a complex species? As we have seen, selection within a single race is without effect. But if we make selections among the individuals of a mixed collection of races, such as Fig. 5 shows, we reach most instructive results. By making our selections in the proper way, we for a time make steady progress toward a certain goal. We will suppose that we do not know of the existence of these races; this is the case with most experiments in selection. From the species as a whole, as shown in Fig. 5, we will select for increased size. Let us follow the old plan of selecting many individuals showing the desired character; we will preserve all specimens above the mean size of the entire collection. That is, we divide the collection at $x - x$ rejecting all those to the right. By so doing it is evident that we exclude all specimens of the two smallest races *c* and *i*, while preserving the majority of the specimens of the larger races. Allowing these to propagate, we of course get a mixture of the remaining larger races; hence the mean size of the whole collection will be greater than at first. Selecting again those above the mean size of this lot, we drop out another small race, and the mean of the collection as a whole again rises a little. We are making good progress in the improvement of our species. By taking successive steps of this character, dropping out the smaller races, first partly, then completely, one after another, we can for a long time continue to improve by

selection. But finally we reach a stage in which all but the largest race have been excluded. Thereafter we can make no farther progress. In vain we choose for breeding the largest specimens of the lot; all belong to the same race, so that all produce the same progeny. Selection has come to the end of its action.

It is well known that this is a course of events commonly observed in selective breeding. Improvement occurs for a time, then stops. We might have produced the final result at once, in our infusoria, by merely isolating at the first selection the largest individual of the entire lot; its progeny would have produced at once a pure race of the largest size attainable. Selection here consists simply in isolating already existing races; it produces nothing new.

Thus the facts in Paramecium furnish an excellent illustration, in the simplest possible form, of the principles of breeding for improvement so convincingly set forth in de Vries's recent work on plant breeding, and in his other writings.

It is well known that in inheritance extremely marked parental characters appear less marked in the progeny; the progeny of extreme parents are on the whole nearer the mean than were the parents. This fact is spoken of as regression. The reason for this is clear in such a collection as Fig. 5. Suppose we breed from the very largest specimens of the entire collection. These are the largest individuals of the largest race. They produce, as we have seen, like any other specimens of that race, progeny of merely the mean size for that race. The progeny will then of course be on the average smaller than their parents, but they will be above the mean size of the species as a whole, since they belong to the largest race. Thus "regression is not complete"; the progeny diverge from the parents toward the general mean of the species, but do not reach it. If however we consider a single pure race alone (Fig. 4), and breed from the ex-

tremes, then "regression is complete," since the progeny are of the mean size for the race as a whole.

Work with "pure lines"—where no intercrossing of races or individuals occurs—is possible with but few organisms, and little of it has been done. In the few investigations carried on in this way, the same conditions have been found that we have set forth above for Paramecium. They were first shown by Johannsen[6] to hold for beans and barley, and later by Elise Hanel for Hydra.[7] The fact that there exist diverse races, tending to breed true, has of course been shown for many species, but in most cases it is difficult to maintain pure lines, and thus to absolutely demonstrate the relations above set forth, as has been done for beans, barley, Hydra and Paramecium. In the Protozoa it has of course been possible to carry the work through an immensely greater number of generations than in many celled organisms. The extremely important work of Barber[8] has shown the same condition of affairs to exist in yeast and bacteria, though with certain additional factors to be mentioned later.

When we deal with organisms that continually intercross, the conditions of course become immensely complex. Each individual represents, as it were, many diverse lines, whose appearance and disappearance in the hide-and-seek way characteristic of Mendelian inheritance makes interpretation extremely difficult. There is not wanting evidence that the same principles are at work even here; that the results of the study of "pure lines" give the clue by the aid of which the more complex results of selection in biparental inheritance may be unraveled. If this is the case, then selection would act even here also by isolating diversities that already exist, not by producing diversities. There are of course some not

[6] Johannsen, W., "Erblichkeit in Populationen und in reinen Linien," 68 pp., Jena, 1903.

[7] Hanel, Elise, "Vererbung bei ungeschlechtlicher Fortpflanzung von *Hydra grisea*," *Jenaische Zeitschr.*, 43, 1907, pp. 321–372.

[8] Barber, M. A., "On Heredity in Certain Micro-organisms," *The Kansas University Science Bulletin*, 4, 1907, 1–48, pl. 1–4.

yet thoroughly analyzed facts that are difficult to interpret on this basis, so that its general adequacy remains to be determined.

The work with Protozoa emphasizes further certain important points regarding *variations.* The interest of studies in variation lies mainly in the assumption that the variations are heritable, supplying material for selection and evolution; this assumption is openly or tacitly made in most work on the subject. Yet when we actually determine how far this is true, we find (as we have seen) that in a pure race of infusoria *all* the differences between individuals are environmental and without significance in inheritance. If we study these variations by biometric methods and laboriously work out numerical coefficients of variation (as the author has done on a large scale in his original paper) we acquire data which are perhaps not without some sort of interest, but which have no bearing on inheritance or selection or evolution. The "standard deviation" and "coefficient of variation" express in a pure race mere temporary conditions, of no consequence in heredity. If we could make all conditions of growth and environment the same throughout our pure race, all the evidence indicates that the standard deviation and coefficient of variation would be zero, and this is the positive value of their assistance in determining what shall be the characteristics of the progeny.

Even when we deal with mixtures of diverse races the coefficient of variation is, as a rule, mainly determined by differences due to growth and environment. "Wild" cultures of Paramecium, consisting of many races, may not give higher coefficients of variation than those obtained from pure races. The coefficient of variation is then by no means an index to the permanent heritable differentiations in a collection; its value may be high when there are no such differentiations, or low when such differentiations exist. The important question for all such work is: What diversities are heritable, what are not? This is an experimental question, and the rôle of statis-

tics in answering it is a most subordinate one. When an author deals in standard deviations and coefficients of variation, the first question the reader should ask is: Has the author determined what part of the diversities thus measured have any bearing on heredity? They may have absolutely none.

Thus the mere fact that observable variations exist between individuals can not properly be appealed to as furnishing material for selection and evolution, as has been so generally done. Most such variations have in the organisms studied absolutely no bearing on the evolutionary process, and there seems little doubt but that this is true for organisms in general.

Illustrations of the practical bearing of these points may be found without departing from the particular organism with which we are dealing. It has been shown that the two products of the division of a single individual Paramecium often differ in size at a given time, so that "variation" occurs in non-sexual as well as in sexual reproduction.[9] But these "variations" are mere temporary fluctuations, without effect in heredity, so that their relation to evolution is *nil*. Again, Pearl[10] showed that conjugants are less variable than non-conjugants. This is true even within the limits of a single race, as I can confirm from extensive studies. But all the variations in such a case, both in the conjugants and non-conjugants, are purely temporary matters, without effect on posterity; so far as evolution or heredity or selection goes they can be left quite out of account.[11]

Comparative studies have often been made of the variability of higher animals under different methods of reproduction, under different conditions, etc.; the varia-

[9] Simpson, J. Y., "The Relation of Binary Fission to Variation," *Biometrika*, 1, 1902, 400–404. Pearson, K., "Note on Dr. Simpson's Memoir on *Paramecium caudatum*," *Biometrika*, 1, 1902, 404–407.

[10] Pearl, R., "A Biometrical Study of Conjugation in Paramecium," *Biometrika*, 5, 1907, 213–297.

[11] This of course is no criticism of Pearl's paper, which is one of the foundational ones for this line of work. When different races are present, the less variability of the conjugants is of the greatest significance.

bility of parthenogenetic generations has been compared with that of sexual generations, and the like. These have no meaning for evolutionary questions unless we know whether any of the diversities are heritable. In general, it would appear that most observed variations are *not* heritable.

Perhaps more important even than the distinction between temporary modifications and really heritable differences is another point regarding "variations." Even leaving aside the temporary modifications, much discussion of variation assumes that the word implies an actual *change* from one condition to another. This is obviously a very different matter from mere observance of two different conditions in different individuals. If our object is to discover how far we have actually observed evolution *taking place,* the distinction between variation as an active change and variation as an existing condition (of permanent differentiation between two races) is absolutely fundamental. Evidently, observation of the mere fact that permanent differentiations exist between races is a totally different matter from observation of the changes by which evolution occurs; it is compatible with almost any theory of the origin of diversities; for example, with that of special creation. As a matter of fact, do we find the existing races changing or permanent? What light does our study of variations throw on this?

In Paramecium, in the extensive study of many races for hundreds of generations by exact statistical and experimental methods, *not one single instance was observed of variation in the sense of an actual change in a race.* In the detailed paper, coefficients of variation are given almost by the hundred, and permanent diversities of race are registered minutely and in numbers. But these mean nothing so far as real change in any race is concerned. So far as the evidence goes, every race was essentially the same throughout the work, and may have been the same for unnumbered ages before.

For clear thinking it is of the greatest importance to distinguish variation as a process from variation as an existing static condition of diversity. If this distinction is not made, we may delude ourselves into thinking we have seen evolution occurring, when all we have seen is the complexity that induces us to invent the theory of evolution. The difference is just the difference between seeing a problem, and seeing its solution; between asking a question and answering it.

But is there indeed no evidence that actual racial changes occur in unicellular forms? On this point we have the extremely important work of Barber.[11] Barber was the first to undertake in bacteria and yeasts the study of "pure lines"—of races derived entirely from a single individual. In general his results were the same as those set forth above for Paramecium. Many races of yeasts and bacteria exist, and these races are constant (with the exceptions to be noted). Environmental effects were not inherited, and long continued selection was of no effect in changing such a race. Barber studied also unusual individuals; he found, just as I have set forth above for Parameicum, that their peculiarities were, as a rule, not inherited. But he did find a few cases of peculiar individuals *within a pure race,* that transmitted their peculiarities to their descendants. Here we have then actual changes in a race; variations in the dynamic sense. In this way there were produced races of yeasts having cells of a different form; races of bacteria composed of longer rods than the parents. But such cases were *extremely rare.* Variations that perpetuate themselves were found only in one individual among thousands. Barber's work goes as strongly as my own against the significance of the common variations among individuals—such variations as are measured by the coefficient of variation—for heredity or evolution.

To recapitulate, we find that the unicellular organisms are made up of numerous races, differing minutely but

[11] *Loc. cit.*

constantly. The individuals of any race vary much among themselves, but these differences are matters of growth and environment, and are not inherited. What is produced in reproduction depends on the fundamental constitution of the race, not on the peculiarities of the individual parent. The fundamental constitution of the race is resistant to all sorts of influences; it changes only in excessively rare instances, and for unknown causes; in a study of thousands of individuals of Paramecium, through hundreds of generations, hardly a single case of such change was observed.[12] Most differences between individuals are purely temporary and without significance in inheritance; the others are permanent diversities between constant races. Systematic and continued selection is without effect in a pure race, and in a mixture of races its effect consists in isolating the existing races, not in producing anything new.

To give in brief an account of the general results of extensive work, it is necessary to make definite statements, and to omit conditions, exceptions and qualifications. This the reader is asked to remember; the details may be found in the original papers. The results are based on study and measurements of more than 10,000 individuals of Paramecium, kept under experimental conditions for many generations. But science is essentially incomplete and its results at any time are not final. The author expects to make strenuous attempts to overthrow the generality of some of the results set forth.

[12] A single doubtful case is described in the first of the author's two papers: certain individuals of a race acquired a hereditary tendency to remain united after fission, while others did not show this tendency, or showed it less strongly.

THE COLOR SENSE OF THE HONEY-BEE: IS CONSPICUOUSNESS AN ADVANTAGE TO FLOWERS?

JOHN H. LOVELL

In 1895, Professor Felix Plateau, of the University of Ghent, began the publication of a long series of papers, in which he asserted that Hermann Müller, in formulating his theory of the evolution and use of floral colors, had been misled by a too vivid imagination; and that anthophilous insects are attracted chiefly by odor. In a list of his papers prepared by himself and now before me Plateau states that his latest contribution, entitled Les insects et la couleur des fleurs,[1] contains a "summary of the whole." The conclusions of many years of patient research are given at the close of this paper as follows:

> "In the relations between the insect fertilizers and entomophilous flowers, the more or less bright coloration of the floral organs has not the preponderating rôle which Sprengel, H. Müller and their numerous adherents have attributed to them. All the flowers in nature might be as green as the leaves without their fertilization being compromised. The sense of smell so well developed among most insects far from being a secondary factor is probably the principal sense which discovers to them the flowers containing pollen and nectar."

By fertilization Plateau doubtless means pollination, for fertilization is an entirely distinct phenomenon, often not occurring until many months after the pollen has been placed upon the stigma. Plateau's conclusions have not met with general acceptance; and in some instances, as he himself naïvely remarks, have been criticized in a "merciless manner."

Floroecology is, however, greatly indebted to him not only for many very interesting observations and experi-

[1] Plateau, F. Les insects et la couleur des fleurs. *L'Année Psychologique*, 13, 67–79, 1907.

ments, but also for insisting that the whole subject of the relations of insects to the colors of flowers should be reexamined and tested experimentally. With the exception of the criticisms of Bonnier, in 1879, Müller's doctrine had remained unquestioned, for no other theory of the significance of brilliant floral leaves is so satisfactory as that they serve as signals or flags to attract the attention of anthophilous visitors. It is well to recall that the great authority, which has been attached to the name of Müller, rests on innumerable observations and collections, which were continued up to the morning of his sudden death from a pulmonary complaint while studying the flowers of the Tyrol. He is still justly regarded as the foremost of florœcologists. Says his biographer Ludwig:

> "He is not dead, he lives and will live so long as a flower enraptures the eye of an investigator. His bright spirit will live on and, we hope, like that of his teacher and friend Darwin long be a light on the way to truth in the heart of nature."[2]

Plateau's first paper dealt chiefly with the concealment of the flowers of the dahlia with green leaves; and his second, which appeared in the following year, with the removal of petals. In the last-named communication he describes how he removed the larger part of the corolla of *Digitalis purpurea, Lobelia erinus, Œnothera biennis, Ipomœa purpurea, Delphinium ajacis,* and *Antirrhinum majus;* and with the exception of *A. majus* found that the inconspicuous stumps were visited by insects almost as frequently as the unmutilated flowers.[3] He, therefore, concluded that neither the color nor the form was important, and that insects were attracted by the fragrance alone. I shall again refer to these experiments after relating my own, which gave very decisive results diametrically opposed to those of Plateau.

[2] Ludwig, F. Das Leben und Wirken Professor Dr. Hermann Müller's. *Botanisches Centralblatt,* 17, 404, 1884.

[3] Plateau, F. Comment les fleurs attirent les insects, II. *Bul. Acad. roy., Bruxelles,* 32, 504–34, 1896. I have not been able to obtain this paper, the reprints being exhausted. The experiments are described, apparently with sufficient detail, in Knuth's Handbook of Flower Pollination, and it is upon this account that I have depended.

To determine the influence of the petals of the common pear, *Pyrus communis*, upon the visits of the honey-bee, *Apis mellifera* L., a medium-sized tree in full bloom was selected for observation. The day was clear, warm and calm, the bees were numerous and no other insects were present.

A cluster of seven blossoms near the end of a branch was watched for fifteen minutes and received eight visits of the honeybee. The petals were now all removed and it was observed for a second quarter of an hour. Though a number of bees flew near by, it received not a single visit. During a third fifteen minutes there were two visits, due in part to association, for the bees came from other blossoms on the same tree, which had proved the first source of attraction.

Two other clusters of flowers, growing side by side but nearer the bole of the tree, consisting each of eight flowers, were observed for fifteen minutes and sixteen separate visits of the honeybee were noted The petals of one of these clusters were now removed. During fifteen minutes the adjacent cluster, which still retained its petals, received eleven visits, while not one was made to the cluster without petals. In one instance a bee hovered over it but did not alight.

These results were much more conclusive than I had expected; for, in the second experience, it might have been supposed that the odor exhaled by the evaporating nectar of the denuded blossoms would have attracted the bees, which were only an inch or two distant; but their movements were evidently determined almost entirely by the presence of the petals.

On a warm pleasant morning in August at 11:30 o'clock, (A.M., I selected for experiment two groups of flowers belonging to *Borago officinalis*, or the common borage. They were distant apart about six inches; one contained five flowers; the other, which was at a little higher elevation, contained four flowers. They were both watched for ten minutes. The first received fifteen visits from

the honey-bee, the second thirteen visits. The location of my apiary not far away furnished a large and continuous supply of visitors. The rotate corollas, together with the cone of black anthers, the stamens being attached to the base of the petals, were now removed from the five flowers of the first group. There remained the green calyx, the pistil, and the green disc surrounding it which secretes the nectar. The two groups were now observed for a second ten minutes, the first received no visits, the second seven visits from the domestic bee as previously. Once a bee hovered around the denuded flowers of the first group but failed to alight. The much smaller number of visits made to group number two during the second interval may in part have been due to the less conspicuousness of the whole patch of flowers. There were scattered upon the ground many partially withered corollas and twice a bee was seen to fly down toward them. With a lens of twenty diameters I examined three of the defoliated blossoms and in two of them found eight or nine small drops of nectar, so that had a bee alighted upon them it would have been richly rewarded for its discernment. The flowers possessed no perceptible odor. Three points in the second part of this experiment should be carefully noted; first, that the flowers from which the corollas had been removed, though they contained an abundance of nectar, received no visits; second, that the flowers left complete received a much less number of visits than during the first interval; third, that the bees were attracted by the wilting corollas lying upon the ground.

On August 14, I made the following experiment upon a staminate flower of the garden squash, *Cucurbita maxima*. The weather was clear and warm. During an observation of ten minutes it received twelve visits, eight of which were made by honey-bees and four by workers of *Bombus terricola* Kirby. The perianth was then removed close to the cup-shaped reservoir, but the denuded flower with its prominent club of stamens and yellowish disc was still

a conspicuous object though much less so than before. It was watched for a second ten minutes and received only one visit, from a bumblebee (*Bombus terricola*). During the first interval no visit was counted that the bee did not enter the corolla and go down to the honey receptacle. Within a few inches of this "stump" and a little lower down there was another squash flower, the corolla of which had wilted and was nearly closed. During the second ten minutes this flower received five visits,[4] two from *B. terricola* and three from honey-bees, though they were unable with a single exception to find an entrance. There can be little doubt that had the corolla been present on the first flower these bees would have entered it.

On the fifteenth, the weather being favorable, the experiments on the flowers of *Cucurbita maxima* were continued. Two flowers, both staminate, growing side by side, their corollas touching, were selected. Number one appeared rather older than number two, which had evidently expanded very recently. Both were observed for ten minutes. Number one received six visits, four from *Bombus terricola,* two from the honey-bee; while number two received thirteen visits, all from bumblebees (*B. terricola*). The fresher condition of this flower probably accounted for the larger number of visits. Both the calyx lobes and the corolla were now cut away from number two, the most attractive flower, leaving only the disc and the monadelphous club of stamens. This was by no means an inconspicuous object, as the yellowish disc is 15 mm. in diameter, and the yellow anthers are over 2 cm. long. The two flowers were watched for ten minutes. No visits were made to number two; but number one received twelve visits, six from honey-bees and six from *B. terricola.* It is evident that the corolla was a great advantage, and that number one suffered in competition with number two, the number of visits to number one greatly increasing when number two was rendered comparatively incon-

[4] The bees alighted upon the corolla and tried to enter it.

spicuous. Shortly after this experiment was completed a honey-bee was seen to visit the decorollated flower of number two; and inserting its tongue through one of the narrow slits in the top of the cup-like receptacle it remained sucking for two minutes, finding evidently an ample quantity of nectar. It then visited flower number one, but its further flight was not followed. A moment or two later a honey-bee was again seen on the nectar receptacle of number two, which was doubtless the same individual, for its subsequent flight was followed and it returned twice afterwards, finding the nectar here more abundant than in the complete flowers. Later a fifth visit was observed, probably by the same bee. There were many more bumblebees present than honey-bees, and the greater capability of the honey-bee in finding the nectar and in making the most of its discovery is noteworthy. During this whole time number one, from which the corolla had not been removed, continued to be frequently visited by bees. The corolla of the squash possesses an agreeable fragrance, but the defoliated flower also exhales a strong though coarser and more weed-like odor. The visits were recorded on the instant they were made.

In these experiments the visitors were not a miscellaneous group of insects belonging to several orders and differing widely in their habits of visiting flowers and, according to Müller, in their color sense; but the flowers of *Pyrus communis* and *Borago officinalis* were visited by *Apis mellifera* alone, and of *Cucurbita maxima* by *Apis mellifera* and *Bombus terricola,* allied species, which are placed by some authors in the same family. The visits were purposive and not ambiguous, as is not infrequently the case with the visits of many diptera and even of the less specialized bees. To the complete flowers the number of visits were numerous and decisive. On the contrary, they ceased almost entirely to the decorollated flowers, though they contained an ample supply of nectar; while at the same time in the control observations made for the purpose of comparison they continued numerous. The

few exceptions may be explained by the odor of the evaporating nectar, and by the tendency of bees to return habitually to a place where they have once obtained food. That the white, blue and yellow corollas were beneficial to the flowers of their respective species does not admit of question. To attribute this advantage to any other cause than conspicuousness would appear to be a perversion of the facts.

Let us again refer to Plateau's experiment with *Digitalis purpurea.* The larger part of the tubular corolla was cut away leaving a cup-shaped stump 1 cm. long, which was visited by two bees, *Bombus terrester* L. and *Anthidium manicatum* L., nearly as frequently as when the flower was complete. Knuth suggests that the nectar now being exposed to the sunshine and wind must evaporate more rapidly, give out a stronger odor, and should attract more insects than when it was concealed at the bottom of the long corolla-tube. As this was not the case, he holds that the uselessness of the bright corolla was not proved. I should explain the continuation of the visits of the two species of bees as follows. A cup-shaped flower 1 cm. long is by no means very inconspicuous *per se.* The bees had already visited these flowers and learned that they contained nectar; and they would come again to the same place in accordance with their well-known custom of returning habitually to a locality where they have once procured food. They would find smaller, more open flowers with perhaps a stronger odor; but that insects with the keen discernment of bees should be greatly deceived by this change is highly improbable. The results observed by Plateau in the excision of the corolla of *Digitalis purpurea* are precisely those which would have been expected. The force of this objection occurred later to Plateau himself in the case of flowers masqued with green leaves, as when he enveloped with the leaves of rhubarb the inflorescence of Heracleum, for he says:

"Or, j'ai effectué en 1895 et 1896, aux débuts de ma longue serie de recherches sur les rapports entre les Insects et les fleurs, des expériences

que l'on n'a certainement pas oubliés et dan lesquelles je constatais de multiples visites d'Insects à des fleurs dont toutes les parties colorées étaient cachées par du feuillage. L'objection que les résultats de ces expériences ancienne étaient précisément et exclusivement dus au souvenir de l'emplacement se présente immédiatement à l'esprit."

" Je reconnais bien volontiers que cette objection frappe juste pour certaines des expériences en question."[5]

But in my experiments with the heads of simple dahlias masqued with grape-leaves, Plateau continues, the memory of a place visited habitually does not wholly explain the behavior of the insect visitors. In some instances he covered up only the disc florets, leaving the ray florets exposed; in others he covered the entire upper face of the capitulum, both ray and disc florets, but not the under side, with green leaves, and both bees and butterflies (species of Bombus, Megachile, Pieris and Vanessa) continued to fly toward the inflorescences and often found the pollen and nectar by creeping under the covering of leaves. Plateau concludes that the rays do not act as signals, and that the form and bright colors of the capitula of dahlias are not an important influence in attracting insects.

These conclusions are disputed by Forel, who in the following interesting experiment shows that bees in their visits to covered dahlia heads are guided by both memory and sight.[6] In a dahlia bed containing forty-three floral heads of different colors he covered up twenty-five with grape-leaves bent around them and fastened with pins. Of four others he covered only the discs, while of one he covered the rays, leaving the disc visible. The bees were so numerous that at times there were two or three to a flower. The bees ceased at once to visit the completely covered heads; they continued, however, to fly to the heads with only the discs covered, though they immediately abandoned them, except in a few instances where

[5] Plateau, F. Note sur l'emploi de recipients en verre. *Bul. Acad. roy., Bruxelles*, No. 12, pp. 741–75, 1906. Vid. pp. 771–2.

[6] Forel, August. Ants and Some Other Insects, translated by William Morton Wheeler. The Open Court Publishing Co., Chicago.

they succeeded in finding the central florets beneath the leaves; but to the dahlia with the disc exposed and the rays covered they continued to fly as usual. But the bees remembered the earlier condition of the dahlia bed and seemed to be seeking the dahlia heads which had so suddenly disappeared. Soon a poorly concealed specimen was detected and visited, then another, and at the end of about three hours the entrances at the side and below were discovered and the hidden flowers were again being visited. Forel says:

"Plateau, therefore, conducted his experiments in a faulty manner and obtained erroneous results. The bees still saw the Dahlias which he at first incompletely concealed. Then, by the time he had covered them up completely, but only from above, they had already detected the fraud and saw the Dahlias also from the side. Plateau had failed to take into consideration the bees' memory and attention."

To Forel's criticisms published, in 1901, in *Rivista di Biologia Generale,* Plateau has replied in part: That not only bees but numerous diurnal lepidoptera visited the masqued dahlias, and that while it was freely admitted that insects could see the under side of the covered capitula and the radiating form and red or rose color of the floral ligules, yet they were without attractive value, as it was only very rarely that an insect approached the inflorescence of this side.[7] To these statements I will again refer later. His further explanations as well as his assertions that his opinions have in some particulars been misunderstood by Forel are immaterial to the present discussion. But in admitting that the visits of hymenoptera can be partially explained by memory Plateau practically abandons his position so far as his experiments with dahlias are concerned.

Forel, as has already been mentioned, points out that Plateau has attached too little importance to the bee's memory and attention. These are, indeed, qualities more likely to be appreciated by the practical apiarist than the

[7] Plateau, F. Note sur l'emploi de recipients en verre. *Bul. Acad. roy., Bruxelles,* No. 12, pp. 772–75.

entomologist. A single example will suffice to show the strength of the bee's memory for location. During September and the early part of October, while carrying on various observations, I accustomed honey-bees to visit the window of my library for honey and sugar syrup, and now nearly a month and a half later, though they have not been fed since, they still continue to return whenever warmer weather permits. I have little doubt that when the winter is past and they resume flight in April, as in the experience of Huber, they will come again. I shall certainly expect them.

The great perseverance and power of observation exhibited by bees, when searching for nectar in a locality where they have previously procured it, is likewise well illustrated by Forel's experiment. For more than three hours they continued to look for the missing dahlia flowers, until finally they detected a way to reach them under the leaves. This acuteness of sense is also well shown in the following experiment, which I performed on October 6 after most of the natural flowers had perished.[8]

I accustomed a number of bees to visit a red glass slide, 3 inches long by 1 inch wide, on the center of which was a small quantity of honey The slide was placed in the sunlight on the top of a white box about two feet high. A second white box was then placed fifteen feet from the first and to this the red slide was removed. A bee found the honey at the end of six minutes and a few seconds later another came. In ten minutes there were four bees. During this interval the bees were continually flying around the first white box. I now removed the second white box but left the first undisturbed. An hour later

[8] It is instructive to compare this experiment with one described by Lubbock, where the attention of the bees was preoccupied. "I placed a saucer of honey," he says, "close to some forget-me-nots, on which bees were numerous and busy; yet from 10 A.M. till 6 only one went to the honey." ("Ants, Bees and Wasps," p. 280.) "Attention is surprisingly developed in insects," says Forel, "often taking on an obsessional character and being difficult to divert." ("Ants and Some Other Insects," translated by William Morton Wheeler, p. 21.)

I replaced the second white box, but for the red slide I substituted a plain glass one. A bee found it almost immediately, probably one of the earlier visitors. The slide was now carried to a third position and placed upon an unpainted support fifteen feet from each of the white boxes, the three stations forming the angles of an equilateral triangle. Here it was soon found by two bees. The plain glass slide was then placed on the grass in the center of the triangle, where it was quickly discovered by two bees and a third came a little later. The slide was now placed on the grass fifteen feet outside of the equilateral triangle. It was so inconspicuous that a child, who under my direction approached within a foot of it, failed to see it until a bee alighted in the grass. It required twenty minutes for the bees to find it, and perhaps they would not have done so then had it not been near the route they were pursuing in going back and forth to the hive. It is very evident from this experiment that a force of bees searching for nectar or honey are not easily deceived, but perceive very keenly. The slide was in the sunlight and the attractive influences were the reflected light, the yellow color of the honey (it was goldenrod honey, which is amber-colored), and its odor.

In view of the above observations it can excite no surprise that the bees passed readily under the green leaves which Plateau had pinned on top of the *Dahlia capitula.* The factors by which they were guided were memory and the senses of sight and smell. When the bees returned they found the covered dahlias still in their original position, and though they were not bright colored from above they possessed conspicuousness of size and form; and when the bees in flying about saw the form and color of the rays from beneath and perceived the characteristic odor they recognized promptly the presence of dahlia flowers. Plateau's contention that the form and color of the under side of the capitulum, which was plainly visible, exerted no influence because the insects very rarely approached the head from that side, is without force, for the bees never having found the nectar on the

under side, directed their flight toward the aperture or passageway under the leaves, remembering that the nectar was obtained from the disc flowers. It is not justifiable, says Kienitz-Gerloff, to infer that the color of uncovered flowers plays no part in attracting insects, because when they are covered the odor continues attractive.[9]

Plateau repeatedly mentions that the covered dahlia heads were visited by species of Vanessa and Pieris as well as by bees; but while it is admitted that the mental attributes of bees exceed those of lepidoptera, yet the conclusion that the latter were influenced by odor alone is unwarranted. When a butterfly thrust its proboscis beneath the leaves it showed perception of the form of the inflorescence and memory of the location of the nectar. In the following experience the butterflies exhibited keener powers of observation than some of the less specialized hymenoptera. The flowers of *Iris versicolor* are pollinated by bees; and the nectar, which is secreted at the base of the sepals, is protected by the arched petaloid styles, so that it can not be obtained by butterflies in the legitimate way. I have seen *Pamphila mystic* Scudd. standing on the ovary below the perianth and sucking the nectar through the crevice between the sepal and the style; while the larger banded red butterfly, *Limenitis disippus* Godt. obtains the nectar in the same way from above. On the other hand, an hymenopter, which escaped capture, carefully examined the center of two flowers but failed to locate the nectar. There is good reason, then, to infer that the butterflies in Plateau's experiments were influenced by the position and form of the dahlia heads and the color of the rays below as well as by the odor. The criticism of Kienitz-Gerloff is also as applicable here as in the case of bees.

The experiments of Plateau with covered dahlia heads, therefore, were not well adapted for the purpose intended, and afford an insufficient basis for drawing the conclusion that bright coloration is not advantageous to flowers.

[9] Knuth, P. Handbook of Flower Pollination, 1: 205.

VARIATION IN THE NUMBER OF SEEDS PER POD IN THE BROOM, CYTISUS SCOPARIUS

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WHILE at Wood's Holl in August, 1907, I collected about 100 pods each from a series of 23 bushes of the broom *Cytisus scoparius*. On a vacant lot not far from the Marine Biological Laboratory the plants were growing vigorously, completely covering the space with bushes, many of which were higher than a man's head, and with stalks about an inch in diameter at the base. The material was gathered for an investigation of the relationship between the number of ovules formed and the number of seeds developing per pod. But when the counting was taken up the determination of the number of aborted ovules proved so difficult that I feared the results would be untrustworthy and gave up the project. While working over the data I noticed that Pearson[1] has recorded a series of countings of broom from an English locality, and it has seemed worth while to compare the two lots of material.

Many biologists have held the opinion that changed conditions of life, such as may be supposed to prevail when a species is transferred from one habitat to another, imply an increase in variability. The theories concerning the reason for this phenomenon need not be discussed here. I think the general idea will be familiar to all. I think about the only attempts to determine quantitatively whether there is any increase in the variability of a species when introduced into a new habitat are two studies by Bumpus. He first considered the variability of the egg of the introduced sparrow[2] and concluded that it is decidedly more variable in the United States than in its

[1] Pearson, K., and others, *Phil. Trans. Roy. Soc. Lond.*, A, 197, 335, 1901.

[2] Bumpus, H. C., "The Variations and Mutations of the Introduced Sparrow," Biol. Lect. Mar. Biol. Lab. Wood's Holl, 1896–97, 1–15.

native country. In judging Bumpus's data on the directly measurable characters by the standard deviation instead of the range of variation Pearson[3] concluded that the American egg is not more variable than the English but rather less so when a more representative English series is taken. It is quite impossible to determine from the color and shape appreciations whether Pearson's English or Bumpus's American series is the more variable, but it seems to me upon rereading Bumpus's paper that he makes a very good case for a greater variability in color and shape of the eggs of his American as compared with his English series. However, Pearson's suggestion of a possible change in the color of the egg must be remembered. Vernon[4] considers the American eggs more variable in shape and color.

Bumpus's second attempt to secure data upon this question was with the introduced Littorina.[5] He found from an examination of three English and ten American series, each of about one thousand individuals, that the American shells are much more variable than those from the British Isles. Duncker[6] who has reworked the data to express the variability in terms of the standard deviation and theoretical instead of empirical range agrees with his conclusions.

The results reviewed above indicate that more data on this question are much needed. Although his conclusions were based upon somewhat unsatisfactory statistical methods Professor Bumpus deserves very large credit for his thoroughly pioneer attempts to solve some of the problems of evolution in the only way in which they can be solved—by the collection of pertinent quantitative data. The problem of variation is such a complex one

[3] Pearson, K., "Variation in the Egg of the Sparrow," *Biometrika*, 1, 247–249, 1901.

[4] Vernon, H. M., "Variation in Animals and Plants," New York, 1903.

[5] Bumpus, H. C., "The Variations and Mutations of the Introduced Littorina," *Zool. Bull.*, 1, 247–259, 1898.

[6] Duncker, G., "Bemerkung zu dem Aufsatz von H. C. Bumpus: The Variations and Mutations of the Introduced Littorina," *Biol. Centralbl.*, 18, 569–573, 1898.

and sources of error are so numerous that great stress is not to be laid upon the results of the examination of a single series of material, but all conclusions must be tested repeatedly and on widely dissimilar organisms. The present lot of broom deserves consideration in this connection.

Cytisus is a native of Europe which has been reported from several localities in the United States. Mr. Vinal N. Edwards writes me that he started the colony from which my collection was taken in 1887 when he set out forty small plants which he dug up on Naushorn Island. In 1898 it was all cut down level with the ground when it came up thicker than ever. He thinks it was first planted on Naushorn Island some fifty years ago.

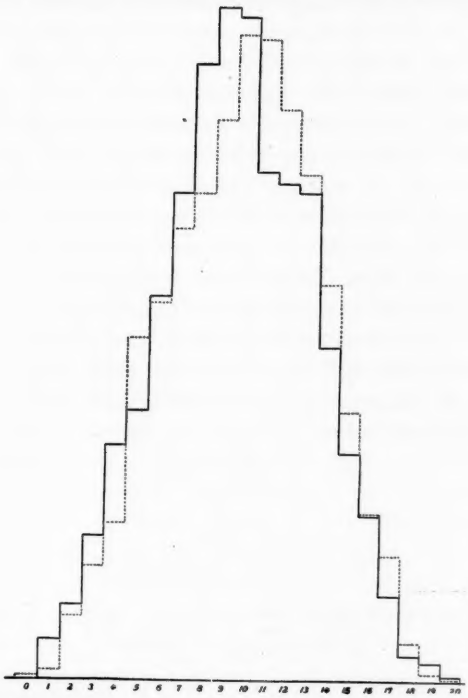
It seems hardly worth while to look farther for the ultimate origin of the colony since we have only a single series of European data for comparison. Several years ago Pearson collected ten pods each from a series of 120 plants at Danby Dale. To render his series readily comparable with my own I have multiplied his frequencies by

TABLE I

VARIATION IN NUMBER OF SEEDS OF BROOM

Seeds per Pod.	Danby Dale, England.	Wood's Holl, Mass.	Difference.
0	—	2	— 2
1	15	4	11
2	28	24	4
3	54	43	11
4	88	59	29
5	101	129	—28
6	144	142	2
7	183	170	13
8	235	183	52
9	254	213	41
10	250	244	6
11	192	242	—50
12	186	216	—30
13	183	190	— 7
14	125	149	—24
15	89	101	—12
16	61	63	— 2
17	32	47	—15
18	9	14	— 5
19	7	3	4
20	2	1	1
Totals	2,239	2,239	

the ratio 2,239/1,200 and placed them beside mine in Table I. The character of the pods is also shown graphically in the diagram where the solid lines represent the English and the dotted lines the American pods.



I think these polygons agree remarkably well. The empirical range is essentially identical. In both cases the highest class is 20. Pearson found no pods with an entire absence of seeds in the 1,200 which he examined, though he suggests that such may exist; I found 2 in the 2,239 of my lot. At first the differences between the frequency of pods in the individual classes, as shown in the fourth column of the table, and graphically in the diagram, seem rather large. But we must remember that two series of countings from the same individual would show many chance differences in their frequencies, and

that neither of the series with which we are dealing is large enough to give very trustworthy results for the frequency of individual grades. We might avoid to some extent the difficulties introduced by the errors of random sampling by graduating the observed frequencies by some satisfactory fitting formula, but it does not seem profitable to take up the labor of curve fitting on the available data. We may, however, calculate the means and variabilities with their probable errors. The constants and their differences appear in Table II.

The means show that the Wood's Holl plants have about three tenths of a seed more per pod than the Danby Dale series. This is to be expected from the diagram where the polygon for the American series is seen to lie a little further to the right than the English. But the difference is only about four times its probable error and so only doubtfully significant even for the samples in hand. I think no one can examine these results and not be convinced that so far as is shown by the physical constants

TABLE II

COMPARISON OF STATISTICAL CONSTANTS OF BROOM

	Average and Probable Error.	Standard Deviation and Probable Error.	Coefficient of Variation.
Danby Dale	9.6425±.0691	3.5466±.0488	36.780
Wood's Holl	9.9982±.0502	3.5236±.0355	35.242
Difference	—.3557±.0854	—.0230±.0603	—1.538

the two collections, one gathered in England and the other in America and counted and reduced by independent observers, are practically identical when we have regard to the probable errors of random sampling. And this notwithstanding the fact that the age of the plants, the number of plants involved, the ancestry of the individuals, and the climatic and soil conditions under which they grew are not taken into consideration or allowed for in any degree! If the constants were based on some character which the qualitative biologist would guess to be little influenced by the environment one might not be surprised at their close agreement; but we are dealing with

a character dependent not merely upon the internal and external factors determining the form of all plant organs, but upon the environmental factors influencing the chances for fertilization as well. Furthermore, it may be noted that we are dealing not with a little variable character, but with one having a coefficient of variation of about thirty five per cent. This is about two or more times the value of the coefficient of variation of the ordinary vegetative characters of plants, but not an extraordinarily high value for seed numbers, as determined from large series of unpublished data.

Summarizing the results of this note, I think we may say that so far as is shown by this one series of material Cytisus is no more variable in the habitat to which it has been very recently introduced than it is in one of its native habitats. As a matter of fact it is slightly, though not significantly, less variable at Wood's Holl than at Danby Dale. Possibly the sensible identity of the variability of the two samples may be due to the small number of individuals which furnished my series of data. These in their turn were probably derived from very few ancestors. I attach no great importance to the results. They simply show that so far as the present material is concerned there is no evidence in favor of the theory that the introduction of a species into a new habitat increases its variability. Possibly some other character than number of seeds per pod would have shown an increased variablity. I use this character merely because I had the data on hand as a by-product of some other work and felt that it would be better to let it contribute its bit of evidence on this problem than to throw it away. Possibly as a fellow biologist remarked when I showed him the closeness of agreement of the constants from the two series the result is "purely accidental." There are many possibilities of error in work of this kind. But until we have a large number of series of quantitative data it will be quite impossible to say whether or not there is anything of value in the theory of an increased variability of "introduced species."

PRESENT PROBLEMS IN PLANT ECOLOGY[1]

The Trend of Ecological Philosophy

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That Schimper was a prophet as well as an ecologist of the first magnitude is well attested by this sentence from the preface to his plant geography:

> The ecology of plant distribution will succeed in opening out new paths on condition only that it leans closely on experimental physiology; thus only will it be possible to sever the study of adaptations from the dilettantism which revels in them, and to free it from anthropomorphic trifling, which has threatened to bring it into complete discredit.

The close interdependence of physiology and ecology is being more and more recognized; this is made manifest by a survey of the titles presented to the botanical meetings year by year. Suggestive among this year's titles are: Bog toxins and their effect upon soils; experimentally induced root-regeneration in Parthenium; the relation of evaporation to the treelessness of prairies; are alpine plants exposed to increased evaporation? Titles such as these would have been quite impossible a few years ago through the failure of ecologists to recognize the fundamental necessity of building their work upon physiological foundations. Quite as fundamental but less fully recognized, especially by many physiologists, is the dependence of physiology upon ecology. The increasing sanity of physiological problems is due in large measure to the wholesome influence of ecology. In the old days when physiology was a mere laboratory science, and therefore artificial, no experimental test could be too

[1] A series of papers presented before the Botanical Society of America at the Baltimore meeting, by invitation of the Council.

bizarre to be applied to plants. A thing never to be lost sight of is that evolution has taken place out of doors, and that the contortions of a puny plant in our illy lighted and gas-ridden laboratories do not solve our most important problems. In recent years no physiological work of greater import has appeared than that from the Desert Laboratory, where the direct stimulus to research has been contributed by the desert itself and its ecological problems.

The developments of the past decade, therefore, make it essential that physiology and ecology break down the barrier erected for them in Madison in 1893, where it was declared that physiology is experimental and ecology observational. The ecologist must experiment in order to resolve a natural complex of factors into its individual elements, while the physiologist must be a student of field conditions, if he wishes to deal sanely with the great problems connected with the evolution of form and behavior. Recognizing, then, the interdependence if not the complete identity of experimental ecology and field physiology, it becomes necessary to consider the underlying philosophy that serves as a motive for all research along these lines. The importance of one's philosophy upon his research can scarcely be overestimated, for it determines the problems to be attacked, the methods to be employed, and, on account of the personal equation, is likely to give some color to the results secured. But it is not necessary that the working theory be true; indeed it is often better that it be most untrue, since it may thus lead to the testing of more theories than might otherwise be employed. The fundamental test of a working theory is that it be that one which will stimulate the maximum of discriminative research. There can be given no better illustration of an unproductive theory than the theory of vitalism. This supposes that there is a fundamental difference between the living and the nonliving, hence one would not expect a vitalist to lead in the attempt to create living matter by experiment.

Vitalism, whether true or not, conduces to lethargy, because it assumes a barrier instead of attempting to find if the supposed barrier can be broken down. Thus the mechanistic theory of life is best as a working hypothesis because it leads to decisive experimentation and to the attempt to create living matter, and in this way leads to the solution of many great problems and may some day cause the settlement of that greatest of all problems, the origin of life. On the other hand, vitalism, by assuming to answer the question in a way that transcends the possibility of experimental test, is a hopeless theory and leads to repose and scientific slumber rather than to activity.

While theories of vitalism in whatever form have ever blighted scientific endeavor, they have been especially harmful in ecology. No biologists are brought into closer touch with life than are the ecologists; their whole atmosphere is pregnant with dynamics and the aspect which they have of plants is that of extreme plasticity. The ecologist comes into daily contact with profound changes in plant form and behavior, and he sees ever before him the panorama of succession. What wonder is it that many ecologists have been carried off their feet by vitalism and have dabbled in anthropomorphic similes? And what wonder that, because of this attitude, some of our best biologists have seen naught in ecology but superficial vaporings or scientific nonsense? But the view-point of ecology has been shifting, indeed has largely shifted, and there are reasons for believing that the ecologists are now closer to the problems of to-morrow than many of the other biologists. The rescue of ecology from dilettantism and anthropomorphic trifling, which Schimper so keenly wished for a decade ago, has been essentially realized. It may be of value to outline the steps that have led to the present happy state.

From the beginning one of the greatest of ecological problems has been that of the origin and significance of adaptations. In other days the solution was sought in special creation, one of the most unscientific of all

theories, because altogether subversive of experiment. The entire question was prejudged at the outset. The theory of special creation, however, has not been especially harmful, because it has generally seemed so unlikely as to have received but little support among scientific men. Perhaps the most baneful of all ecological theories has been the Lamarckian theory of direct adaptation. In its day, that is before 1859, it marked a distinct advance, because it was the first significant attempt to displace special creation by something better. The great merit of Lamarckism was the recognition of plasticity, the substitution of a dynamic for a static nature. Had it been generally accepted, it might easily be said to have marked the greatest single step in the advance of scientific thought, but the world was not then ready for dynamic conceptions. The leaven of Laplacian astronomy had scarce begun to work, and the Lyellian geology was as yet unborn.

The evil wrought by Lamarckism is due to its acceptance by modern biologists. It is essentially a vitalistic theory, presupposing that plants and animals have some inherent mysterious power to contravene the ordinary laws of matter. They are supposed to be able to survive hard conditions because able to adapt themselves advantageously. Of course it is clear that those plants which do respond favorably to changing conditions will be most likely to survive, but adaptationists have apparently overlooked the fact that thousands of species must have died because unprovided with an adequate capacity for advantageous response. Their conception of nature is distorted by centering their attention upon those successful plants that appear to have survived because of their adaptations. The depressing effect of the adaptation hypothesis is most obvious in that it has encouraged sterile imaginings as to the advantages of this, that or the other plant structure and has thus discouraged attempts to discover the real facts involved in the origin of such structures.

Evidence against the reality of adaptation in a subjective sense has been accumulating. At first sight the increase of cutin in plants exposed to increasingly xerophytic conditions, or the increased development of air chambers in plants exposed to increasingly hydrophytic conditions look like adaptations, and such changes certainly seem advantageous. However, there are facts that point in another direction. There is no more important source of strength in plants than that afforded by bast and similar mechanical tissues. Yet recent experimenters have failed to get any significant response in the way of great bast development by exposing growing organs to considerable tension. Bast primordia, however, are very plastic and respond readily to changes in moisture. Thus we have in bundles of bast fibers tissues that do not adapt themselves to a demand for tensile strength, although such a response would be highly advantageous; on the other hand, they respond to increased transpiration, although it has not been claimed that bast fibers are of especial value in checking transpiration. Again, increased conduction, whether due to high transpiration or other causes, often results in an increased development of the vascular tract. The advantage of such a modification is at least dubious in xerophytes, but the case is much more striking in such plants as Artemisia, when parasitized by Orobanche. The Artemisia root is stimulated to excessive development by the attack of the parasite, and examination shows that the vascular tract in particular is greatly increased. If this change in the Artemisia root is an adaptation, it is an adaptation for the Orobanche and not for itself, and what adaptationist could expect a plant to be so altruistic as all this? Similar phenomena are seen in fungus and insect galls, and in the cynipid galls in particular, food accumulates in large amount in definite layers around the larval chamber. Can the oak be supposed to be so thoughtful for the insect as to provide it food? Or, if one chooses the other horn of the dilemma, can the insect be supposed to have

learned the habits of the oak, and found just how to tap it? How much more sane it is to regard these and all other plant reactions as brought about through the influence of specific stimuli, treating any advantage that may come (or any disadvantage) as quite incidental to the main problem!

At the present day Lamarckism and adaptation are scarcely as detrimental to ecological thinking as is the misapplication of Natural Selection. The publication of the "Origin of Species" in 1859 influenced biological thought more profoundly than any other work of all history. It compelled the world to accept the doctrine of organic evolution, and it showed most clearly why certain species die and others live. But it shed only a little light on the great questions involved in the evolution of new species. In view of this it seems most unfortunate that the book was entitled "The Origin of Species"; the alternative title commonly printed just beneath in smaller type presents the real thesis of the book: "The Preservation of Favored Races in the Struggle for Life." Perhaps in part because of the title, but more because of Darwin's over-zealous supporters, natural selection has been made a fetish and has been supposed to account for new forms and structures, as well as for their preservation. In other words, it has been erroneously regarded by many as a theory of evolution instead of a means of accounting for the perpetuation or destruction of species previously formed. The theory of natural selection has worked great harm in the ecological study of plant structures. Thorny plants have been supposed to be selected by reason of animal incursion, and such complex things as floral structures have been supposed to be the result of parallel selection on the part of flowers and insects. There is no adequate evidence, experimental or otherwise, for views of this character. Such experimental work as has been done appears to show that the success or failure of a plant rarely depends upon this or that little advantage, upon which natural selection may be supposed to

work, but rather that its perpetuation depends for the most part upon other things than its so-called adaptations. Few more perfect adaptations for their function can be thought of than the digestive glands of insectivorous plants, and yet there is no evidence in support of the idea that such plants have been able to survive by reason of these glands. The evolution of such a complex flower as that of the orchid along lines that are parallel with the evolution of the mouth parts of a special insect requires a nicety of operation that seems staggering, and all the more because the flower, at least, seems to have evolved so far along the lines of zygomorphy as to be a source of disadvantage rather than of advantage, an impossible idea to the natural selectionist. The facts of regeneration show, as pointed out so ably by Morgan, that plants and animals are often in a position to make an instant new reaction to conditions unlike those to which they have ever been accustomed, and that these reactions may or may not be advantageous; in any case, natural selection can have no possible connection with their origin. The trend of the time, especially among botanists, is unmistakably toward the abandonment of natural selection as a theory of evolution, but ecological work is finding a dominant place for it as one of the controlling factors in succession. The student of vegetation dynamics, more, perhaps, than any other, finds displayed before him an incessant struggle for existence; in the changing conditions, the fitness of an old species to remain or of a new species to displace, it is commonly a matter of profound importance in the vegetative change produced.

This is not the place to enter upon a discussion of those evolutionary theories that to-day hold the foremost place. We are awaiting with keen anticipation the noteworthy symposium on evolution that is to make this meeting historic. Suffice it to say that the downfall of the theory of adaptation does not mean the downfall of epigenesis or of extrinsic theories in general. The likelihood of a profound influence of the external world upon the trend

of evolution was never more evident in the past than it is to-day. The work of Klebs has opened up almost limitless possibilities along such lines. The intrinsic theories of evolution, such as orthogenesis and heterogenesis (or mutation) are also vigorously maintained. All such theories, both extrinsic and intrinsic, appear to be in harmony with the present results of ecological research, and the future alone may say whether some or all of these and more are true.

To the working ecologist the necessary consequences of the abandonment of the idea of adaptation and of natural selection as a causative factor are most vital. First and foremost there comes the possibility of disadvantageous trends in evolution. To some extent such tendencies will be checked by the destructive operation of natural selection, so that only such new species as are most fit are likely to survive and have progeny. But in view of the ideas that have generally prevailed in past years, it can not be emphasized too strongly that plants may retain useless structures and even structures that are moderately harmful, and yet live on if they also possess other structures or habits that are sufficiently advantageous. This conception at once relieves ecologists of one of the most arduous of their former duties, the establishment of an advantageous function for every organ, and of a benefit in every function. The chapters on the uses of palisade cells, crystals, poisons, latex and the myriad kinds of hairs are likely to be shorter and less dogmatic in future ecological treatises. Even such organs as stomata are apparently being divested of their erstwhile most important function, the regulation of transpiration.

It has been so long the fashion to regard the various kinds of floral structures as most useful that it may be thought ecological heresy to question their utility. The intimate correlation between the evolution of the insect and the flower was such a pretty story that it seems rude to question it, but do we have any adequate evidence of

advantage in the myriad diversity seen in flowers, much less any advantage great enough to have been of significance in directing to any notable degree the trend of evolution? It is usually assumed that dichogamy, heterostyly, prepotency of foreign pollen, and zygomorphy are advantageous characters because they promote cross pollination or pollination by special insects, but the facts on which such conclusions are based are very slender. There are many plants which are regularly close-pollinated and they seem to succeed as well as others. The Compositæ are often regarded as the highest of the seed plants, and they are of especial interest because they are a group that is ecologically successful as well as morphologically advanced, features that often fail to coincide elsewhere. But the Compositæ show comparatively little zygomorphy or insect selection; as a group they are notably geitonogamous or even autogamous, and yet none of the supposed disadvantages of close pollination are evident. Indeed the massing of flowers in heads and the consequent facilitation of pollination between near-by flowers may be one of the reasons for their great success. But there are reasons for believing that any or all kinds of pollination are vastly inferior to vegetative reproduction in determining the success of a group. The notable success of the grasses and sedges is doubtless due to their rhizomes far more than to their flowers, and in the duckweeds and many aquatics the flower has become almost a negligible quantity. Such considerations make it at least doubtful whether many conspicuous floral structures possess the great advantages in the life of plants that have been commonly ascribed to them.

The conception that plant structures may often have originated quite independently of any important use or function, or even independently of any environmental influence is useful at many points. It explains how there can exist the phenomenon of "over-adaptation," which appears to be exhibited in the orchid flower and in the testa of many xerophytic seeds. It makes possible a new

and seemingly saner ecological classification of plant structures.

The work of Witte seems to show that plant forms may be either obligate or facultative, that is that they may be inherent or may be subject to environmental control. In a xerophytic flora, such as that studied by Witte in Sweden, there are many plants of dwarf habit. Experiment shows that these dwarfs behave very differently in mesophytic conditions. Some develop into tall and luxuriant plants, while others remain as truly dwarf as in xerophytic soil. The dwarfness of the former is facultative, of the latter obligate. The former is clearly a response or reactive xerophyte, owing its form to its surroundings; the latter appears to be an inherent or congenital xerophyte, the cause of whose development is as yet unknown. It is probable that further experiment along these lines will show that many other plant forms apparently identical are most unlike in nature and origin. Time will permit but one further illustration. In mesophytic forests one sometimes finds plants that appear to be xerophytes. A notable example of this is seen in many species of Begonia and Peperomia that grow in the depths of the rain forest. Both in external aspect and in all the details of leaf structure such plants appear xerophytic; it seems almost certain that these plants are congenital xerophytes, species whose xerophytism is stamped upon them to such an extent that age-long exposure to the moisture of the rain forest has not destroyed it. Whether congenital forms in the final analysis differ in any radical degree from reactive forms can not now be told; it may be that all plants are or have been plastic, but it is clear that the recognition of the double possibility in the interpretation of plant structures is at present advantageous.

A minor but necessary matter is that of terminology. One of the unfortunate features about language is that expressions lag behind ideas. Long ago we knew that the heart is not the seat of the emotions, but our language

still retains the old phrases. We continue to speak of the rising and setting of the sun. In like manner we still employ such terms as adaptation, adjustment, accommodation and regulation, although these are vitalistic words which imply that plants and animals can transcend their environment and can contravene the ordinary laws of matter (though it is to be pointed out that the word adaptation is harmless when used objectively). The old-time ecologist was very anthropomorphic and delighted in words derived from φιλέω (I love). Ecological literature is still burdened with such words as xerophile, geophilous and entomophily; particularly objectionable is the word myrmecophily, since it is found that plants merely endure the visits of the ants. Such terms as storage and reserve food appear to imply forethought on the part of the plant and should be abandoned. Words like normal and type are far too freely used, for it can not be emphasized too much that one structure or habit is about as normal or typical as any other. The word function, which is *per se* harmless, has almost come to be a synonym of purpose and may, perhaps, give way largely to rôle. It is not an inconsequential matter that we clothe our ideas with words that are correct and adequate. It is worth the effort, even if we are obliged to substitute a cumbersome though scientific phrase for a euphonious but anthropomorphic word. But of course our language is less important than our thoughts. Our scheme of philosophy is fundamental, for it determines the motive, the scope and the direction of our research. The most blighting of philosophies is that which predicates a maximum of dogma, the most stimulating is that which demands a maximum of experimental test.

DISCUSSION ON PROFESSOR COWLES'S PAPER.

PROFESSOR SHAW: If we should, as Professor Cowles says, discard the word "storage" and, in short, if I understand him correctly, all the words which carry teleological ideas, I should like to inquire what we shall say. What resources of the language shall we use to talk to a class about a starchy tuber and avoid implying purposeful adaptation?

Professor Cowles: It is a difficult question that Professor Shaw asks, I have been working at that for several years, and I have not all of the answer yet, but I have part of it. We now use the word "response," which I am convinced is expressive of no teleological idea. To speak of a response in the living and non-living will answer nearly all purposes, and is entirely free from teleological ideas. The word "storage" is more difficult to handle; personally I use the word accumulation. Take the word "gall," for instance—oak gall; one would hardly teach his class that an oak gall stores, but to speak of food accumulation of an oak gall is not incorrect.

Professor Clements: It seems to me that Professor Cowles puts emphasis on the wrong part of the dilemma. If we change our ideas in the proper direction, it is not at all important what we call them. "Response" implies more of vitalism than adaptation, yet I would adopt the idea and let the word stand.

Dr. Livingston: We sometimes try to cut short our expressions too much, as there is a tendency in all things to adopt shorter expressions instead of long ones, and finally a phrase comes to be a single word, and if the process goes on long enough, a short one. In the present stage of ecology, there is perhaps too much tendency to cut our phrases down to single words before the majority of people who are using the words have yet appreciated what the phrase means, and I am quite agreed with Professor Cowles that we can sometimes find other words, as in the case of accumulation instead of storage, which will express the point; but, I think that in many cases, in order to keep our ideas clear, so that elementary students understand them, we must express the thing in mathematical language, so as to say exactly what we mean. With reference to adaptation, there are one or two points which ecologists have had to study, and of which Professor Cowles makes no special mention, viz., the survival of the fittest and the operation of natural selection in the succession of certain plants. In the survival of the fittest species, for instance—what makes these species the fittest? It is their adaptation to their environment. We may be able to disprove certain specific cases of adaptation that have been passing current and taken for granted for years, but can we get rid of the general idea at all?

Professor Cowles: These are points which I had to leave out of my paper, on account of my limited time. Personally I distinguish between adaptation in the subjective and in the objective sense. It is quite correct to speak in these plants of survival: I object to the use of language implying that these plants adapt themselves in the subjective sense. The use of the word in the objective sense is all right, but the subjective use of it I object to.

Professor Harshberger: Some one has said that our ideas never keep pace with the growth of our language, and our language never with our ideas. That has always been found the case in making hard and fast terminology. Where we assign a particular name to a definite idea and purpose, in a short time our ideas change so that our term has to be made more elastic. Now it seems to me that one of the difficulties always being met with is having to adapt our language to our changing ideas. Would

it not be better to have a less hard and fast terminology, to have a few terms that are generally applicable, and then use in a definite way a description, so that a person, in reading the description, will of necessity get from that description the idea which the author wishes to convey, and instead of building up a vast terminology, we shall have a few simple terms of general application, and apply these terms with latitude, so that with the growth of our ideas, beginners or even the person who has been accustomed to the use of the words, will have a chance to adapt the new ideas to the old terminology?

Professor Bolley: If, as Professor Cowles says, plants respond to stimulation, will he grant that these responses may be hereditary, and if they are hereditary—why is it not adaptation?

Professor Cowles: I would rather not go into this question of heredity. I don't think we know enough about it to ask or answer that. I don't believe it has been proved that there could be such response as is suggested, nor have we disproved it.

PRESENT PROBLEMS OF PHYSIOLOGICAL PLANT ECOLOGY

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By physiological ecology is here meant merely the study of the factors which determine the occurrence and behavior of plants growing under uncontrolled conditions. Field physiology would be almost a synonym for the term here used. Pure physiology proceeds, as far as is possible, by controlling conditions. By varying known conditions and measuring the plant responses definite relations are established between stimulus and response. But ecology must perforce proceed without the known conditions, without the synthetically built-up environment of pure physiological research. Here it is necessary to measure and *analyze* natural conditions and to relate these to the behavior of the plants. The problem of measuring the plant phenomena, the determination of the number, size, form, structure, etc., of the plants involved, is essentially the same for both lines of study, but that of measuring environmental conditions is, of course, much more difficult where the latter are uncontrolled.

There is a principle of scientific research, that in an investigation which involves the measurement of a number of causal factors and the relation of these factors to resulting conditions, the various measurements should be of as nearly equal accuracy as possible. Where a number of complex factors are to be dealt with, as in ecology, progress must come, on the one hand, from a refinement of methods of measurement and, on the other, from better interpretations of the data resulting from these measurements. According to the principle just stated, we should ever seek to improve those of our methods which are the

least accurate, not those which are the most easily susceptible of improvement. It is, indeed, often a waste of energy to seek the highest possible accuracy in *all* of a series of measurements where one or more are at best of low accuracy. The accuracy of the resulting summation must be subject roughly to the error of the least accurate of the members.

It is not my purpose to submit any recommendations as to improvement in the general philosophy of ecology, although we must all realize that one of our greatest hindrances at present lies in the careless thinking which fills our literature with wrong or at least misleading imaginings, such as are suggested by the Jonah-like words, *adaptation, use, purpose,* etc. It is to certain lines along which improved methods of measurement seem desirable that I wish to call your attention at the present time. Our methods for dealing with the plant responses, with the *effects* of environment, already possess a general accuracy far surpassing that exhibited by the methods employed in measuring the environmental conditions which act as causes. I am unable to avoid mentioning, however, one phase of plant measurement which has so far received an almost insignificant minimum of attention, both from physiologists and ecologists. I refer to the subterranean portions of the plant. The relations existing between the environmental factors and the development and behavior of underground stems have been studied for some forms by Vöchting, Klebs and others. Roots have usually been studied in water or in air and only in the last few years has their behavior in the natural medium, the soil, been seriously taken up. A number of agriculturists have attacked the problem here suggested, but of course with reference to cultivated plants. Freidenfeld has made, as far as I am aware, the first attempt at a really broad study of the ecology of roots. The work of Dr. Cannon on the root systems of desert plants shows how extremely important subterranean competition may sometimes be. It would seem

that the underground portions of ordinary plants are well worthy of more attention than has heretofore been accorded them.

We turn now to the environmental factors. When it is sought to determine the causes influencing the behavior of plants growing under natural conditions, two very different methods may be resorted to, the observational and the experimental. By the experimental method we try to determine, on the one hand, the kind and amount of vegetation and, on the other, the magnitude of the various physical conditions which make up the environment. From these two series of observations are selected paired concomitant factors or groups of factors, and when the same concomitants appear in a number of such pairs the conclusion is drawn that the relation between the paired factors is a causal one. By the experimental method we seek to control the conditions to a greater or less degree, either synthetizing an artificial environment (experimental physiology), or growing the same plant forms under various natural environmental complexes. This sort of work may be termed experimental ecology. In so far as the environment is artificially synthetized, it is comparatively easy of measurement, but where natural conditions are allowed to obtain, the experimental and the observational methods both require the measurement of uncontrolled factors, and thus present great difficulties.

The complexity of natural conditions makes it necessary often to break them up into component parts and to measure the parts separately. For convenience in handling, these factors have been classified into climatic and edaphic, but I fail to see that such a classification has any relation to the activities of the plant. I shall, therefore, speak here merely of environmental factors, classifying them, for ease in discussion, into those which are active above the soil surface and those which are active below it. Each group must, of course, be further analyzed according to the purposes of the investigation. But it must be remembered that the data from separate com-

ponent factors usually need to be again summed in order to express the environment as a whole. For the great general problems of plant geography it seems inadvisable to attempt too extended an analysis, rather is it better to seek methods of measurement which will furnish integrated evaluations of groups of environmental conditions. With our present lack of knowledge, the pressing of the analysis too far often results in such a complex of data that an interpretation is impossible. A fairly satisfactory integration of the main air factors seems to be furnished by the atmometer; as to the soil factors, we have made hardly a beginning in this direction. In the following paragraphs I shall first consider the measurement of the air factors, denoting by this term all factors which are active above the soil surface, whether or not the air is actually involved.

Atmospheric Factors.—Atmospheric pressure can be easily measured by means of the barometer, curves are automatically constructed by the barograph. Considering the perfection of this instrument, it is rather unfortunate for ecology that the plant is so little influenced by the natural variations in atmospheric pressure.

Temperature is very important in plant activities, and we have practically perfect instruments for its measurement and for the construction of its curve. Unfortunately we have as yet no well-tested method by which temperature can be interpreted in regard to its effect. A beginning which promises much has been made by Dr. MacDougal with his integration of the thermograph record and Professor Lloyd has told me of a new method devised by him for interpreting maxima and minima. Here lies one of the best fields for the scientific ecologist with a mathematical turn of mind.

Wind velocity can be measured and recorded by means of the ordinary forms of anemometer, but the instruments are not well suited to field work, largely on account of their expense. Perhaps improvement may be forthcoming along this line.

The conditions of humidity, which appear to be so important to plant life, can best be measured directly by means of the dew-point apparatus, but the instrument is not as satisfactory in the operation as could be desired. The whirled psychrometer and the wet and dry bulb thermometer are more easily operated and are quite satisfactory as regards results, especially where the humidities dealt with are not too low. Attention may be called here, however, to the inadequacy of the wet and dry bulb thermometer without a strong current of air. The current should be so strong that any increase in its velocity would produce no further lowering of the temperature of the wet bulb. The hair hygrometer is unreliable unless often standardized by some other instrument. Especially is this so in regions where the humidity is usually low or where its fluctuations are very great. Much improvement is surely possible in connection with this factor.

The evaporating power of the air, an integration of the effects of temperature, wind velocity, relative humidity, and, to some extent, of light intensity, is at least not as difficult of measurement as formerly. The porous cup atmometer can be made to give data for a curve as well as a final integration for a long period. It seems that we may expect much from this or some similar instrument.

Precipitation data are easy to obtain with amply sufficient accuracy, but the factors of superficial and subterranean run-off as well as that of evaporation from the soil surface (all of which are almost hopelessly difficult to measure) make these data very hard to interpret, except for particular localities. Their final interpretation will probably go hand in hand with that of evaporation and soil moisture.

For the measurement of light intensity—a factor which has been shown conclusively to be of prime importance in many ecological problems—we have at present no reliable and practical instrument. The delicate bolometer

would doubtless give the data needed, but it is not well suited to field work and is at best too expensive. The so-called photometers (such as those used in photography) are unsatisfactory in the extreme, both theoretically and practically. They are, of course, not photometers at all, but actinometers, and for our purpose it is to be remembered that the shorter light waves are at least not the most important in plant activity. Here again is a field that should prove wonderfully fertile to him who has the courage and patience to cultivate it.

The determination of the composition of the atmosphere is important in certain lines of investigation and in the solution of general ecological problems in certain regions. For this purpose the methods already at hand are perhaps satisfactory enough, though we are unable to obtain automatic records of fluctuations in these conditions.

Soil Factors.—If the factors active above the soil surface present great difficulties, those active in the soil present greater ones. What knowledge has been gained by the agriculturists is seldom at the disposal of the ecologist, perhaps partly from the nature of the agricultural literature, and partly from a too common feeling that agriculture and ecology are far apart. (It appears to me that ecology is the legitimate and necessary meeting-place for scientific botany and scientific and practical agriculture.) But the agriculturists have not made any very great progress in this field. Their measurements of soil conditions are too often merely determinations of the various amounts of inorganic salts which can be extracted from the soil by one or another cleverly chosen solvent. In some cases determinations are made of the total amount of organic matter in the soil, but it appears that these chemical results lack much in ease of interpretation, so much that they are of little value to the ecologist.

Soils have been classified by various workers according to the size of the component particles, but I have not

found any adequate method of interpretation by which the data of the physical analysis may be made to aid in the explanation of vegetational conditions. There is no doubt that these data contain much valuable information, if we but knew how to interpret them.

A beginning has been made in the important and fundamental inquiry into the attraction of the soil for water and the ability of the soil to conduct water to plant roots, but our ignorance in this regard is even more dense than that concerning the normal physiology of the roots themselves.

The geological origin of soils (a subject which makes up a large portion of the text-books on soils) is of no possible importance in either agriculture or ecology. Mitscherlich—the author of the most scientific book on soils which I have come upon—says in his preface,

> For our cultivated plants the geological origin of the soil in which they grow is in no way important; the growth of the plants must always depend upon the *present* physical and chemical constitution of the soil.

Of course this is just as true of uncultivated forms. But attention needs to be called here to the principle already mentioned, namely, that in the pioneer work in such a field as this it is often not well to analyze the great general factors to too great an extent. Great general vegetational features may be compared with great general soil features, and wonderfully enlightening results have come from such comparisons, as, for example, those obtained by Dr. Cowles and his associates in this field.

The possible importance of small amounts of organic chemical substances in the soil has been strongly emphasized by the work of the Bureau of Soils and by that of Dr. Dachnowski and others, and evidence in this regard is rapidly accumulating from all parts of the world. There is now little reason to doubt that bog soils and others which are poorly drained owe the character of their vegetation in great part to the presence in the soil of toxic bodies. There is evidence that many well-

drained soils contain similar substances. The ecologist can not afford to neglect this important line of advance.

The water conditions of the soil have not received the attention which their importance justifies. For determining the amount of soil moisture our methods are confessedly crude and unsatisfactory, yet they have not been employed as extensively as their accuracy seems to justify. Graphs of the fluctuations in the water content have yet to be constructed, although their construction is comparatively simple and their value for our purpose must be very great. Such curves should replace the bare and almost useless data of precipitation and run-off. Improved methods of measuring soil moisture will of course be of great value, if such can be devised.

As to the rate at which the soil can supply water to the plant—quite a different question from that dealing with the amount of soil moisture—we know almost nothing. This rate of possible supply, or the resistance offered by the soil to water absorption by roots, is, I think, perhaps at present the most important problem in all ecology, and it has hardly been touched upon. But the problems here suggested seem to be as difficult as they are important.

We know almost nothing in a quantitative way about the relations between the oxygen of the soil and plant development. If this field should be developed we should undoubtedly be placed in condition to explain many dark and complicated points. The capillary power of the soil apparently determines, other things being equal, both the rate of water supply and that of oxygen supply, and perhaps the best that can be done here, in the absence of more perfect methods, is to study plant behavior with reference to capillary power and water content. But ecologists have hardly even attempted to relate the easily determined capillary power (which is constant in any given soil) to the vegetation, and it is difficult to foresee what important results might be forthcoming from such a simple study.

The temperature of the soil can be measured and recorded with about as great ease as can that of the air. But we meet here the same difficulties in regard to interpretation.

Finally, for a goodly number of ecological investigations, the bacterial flora of the soil must be investigated. The agriculturists have made good progress here and we may do well to follow them. The possibilities are very great.

In conclusion I should like to call attention to what appears to me to be the one great general need of ecological work, namely, the need of quantitative studies. It is only through such studies that the science of the relation of the plant to its environment can make real progress.

Discussion of Dr. Livingston's Paper.

Dr. Burns: I am heartily in accord with all Dr. Livingston has said, and I have a lot of records cf light readings, that I think I have had for the past six or seven years, that I don't know what to do with. An ecological work, for instance, will dilate on rain force, and then leave that alone, and presently suggest something entirely different. It seems to me that we could work on something in the line of the determination of the maximum and minimum of light, and along this line I have been trying to work out the amount of shade that these plants can endure before they will die out and be succeeded by some other plant, but I have not got on very far.

Dr. Pond: It would be very valuable if we had some work bearing upon an analysis of a given factor in a given case, and it may be interesting to know that a recent article really attempts it. I refer to the article of Ball's on "Temperature and Growth." Of course, temperature is an external condition. Its effect on growth may be either unseen or apparent in some outward manifestation. This article shows, by a careful analysis, that the temperature factor in the specific case which he was working on, namely, a fungus,—the temperature factor as applied produced a substance which inhibited growth of that fungus and finally stopped its growth.

Professor Barnes: May I take this opportunity to say that I hope very much some of the reforms will be adopted, not only by ecologists, but also by some other members of the botanical fraternity. Mr. Harshberger's quotation that our ideas never keep pace with the growth of our language, and our language never with our ideas, has more truth in it than we imagine. Our ideas have not always kept pace with the growth of our language (laughter). It is greatly to be hoped that the language will not be strained any farther. We need no extensive growth of that, and while far be it from a mere editor to suggest to any ecologist that a page of tabular matter not only costs three times as much to set up, but seems

actually useless and trifling, yet I hope that these suggested reforms will become actualities.

DR. LIVINGSTON: In that very connection it occurs to me that perhaps there is another line of ecological work which goes a step farther in clearing up, that is analysis of conditions. What is found out about physical conditions—then comes the question, how do these conditions come into existence? That is, perhaps, a part of the study of ecology. Very often we have to take the analysis back in order to explain how conditions arise; for instance, this plant grows less because of light, heat and moisture conditions. Now I might enquire how these conditions are brought about? By a tree growing alongside or the absence of vegetation—so we see how ecology leads ever to other fields!

DR. GRIFFITHS: I recall, in connection with the gentleman's statement regarding light and heat, a surprising experience I learned of by talking to a commercial gentleman in Arizona—a commercial man but a scientific one at the same time, a gentleman connected with the solar motor industry, of which you have heard a great deal, and I was surprised at the results of his measurement of light and heat, the measurement of heat particularly. He measured heat, of course, in direct relation to his machine—the reflecting surface of his machine—by a thermometer placed in a black box, with its face to the sun, the box simply being an open one, with the open side to the sun. Much to my surprise he informed me positively than an hour's sunlight on the Atlantic Coast was more efficient than an hour's sunlight on the desert of Arizona. Now, that may be an obvious fact to botanists, but it was not to me at the time. I subsequently thought of the matter, and thought possibly I could see reasons for it, but it had never occurred to me before. The result mentioned is possibly due to the presence of a smaller amount of dust in the atmosphere upon the Atlantic Coast. With a heavier rainfall the atmosphere is clearer. The transmission of heat is more certain and undoubtedly his statement was true. He has demonstrated it with his machine. I presume it is due to the presence of a large amount of foreign material in the atmosphere.

NOTES AND LITERATURE

NOTES ON EVOLUTION

THE retirement of Ernst Haeckel from his chair in the University of Jena is a punctuation mark—fortunately not a period—in the long and noble story of "*Haeckelismus in der Zoologie.*" I am aware that the coining of this phrase by Karl Semper and the subsequent use of it by some zoologists and many theologists were not of the nature of compliment to the veteran fighting evolutionist of the Thüringian hills. The phrase was meant to connote reproach, but I prefer to see in it an unavoidable recognition of the great influence and importance of Haeckel's work in the history of biology and evolution. We may decry speculation in zoology and phylogeny in evolution, but without scientific imagination we do not go far forward in any science, and the principles of evolution studied without reference to their practise would leave bionomics far more "philosophical" and much less "biological" than we would have it. Even if Haeckel's speculations and vigorous championship of them had done no more than serve as a stimulus to others to work in order to fight them, they would have had their inestimable importance in evolutionary history. As a matter of fact many of the Haeckelian speculations of the early days are now the accepted and incorporated evolution commonplaces of the present day.

Haeckel gives up lecturing to the Jena students and peering over their shoulders at their dissections to devote himself especially to the building up and care of his new Phyletic Museum. He is now seventy-five years old, and for forty-five years has taught, investigated and written at Jena. Now he gives up part of this work to undertake something else in its stead. A glorious record! And one not uncommon in German scholastic life. Leuckart was lecturing vigorously every day in the week except Sunday up to within two weeks of his death at seventy-six, and the number of active and anything but superannuated professors in German universities beyond the Carnegie fund retiring age is suprisingly large.

The new Phyletic Museum at Jena has been established solely

through Haeckel's personal activity and largely through his personal financial aid. He has given to it 30,000 M. of money and his private library and collections. The building, for which original gifts amounting to 100,000 M. were obtained is now finished and the gathering together and arrangement of collections are going on. It is hoped to have sufficient material on hand and arranged by next spring (1910) to justify the public opening. The building was formally taken over by the University of Jena last July (1908) on the occasion of the celebration of the 350th anniversary of the university's founding. The gathering of the collections and their maintenance must depend entirely in private gifts, and Haeckel makes an earnest appeal to all friends of the development theory for financial aid. Money may be sent to the *Rentamt der Universität Jena, Jenergasse 8, Jena.* Donors of sums of 10,000 M., or over, will have their names engraved on a tablet of "*Ewige Mitglieder des Phyletischen Senates*" placed in the entrance hall of the museum. Professor Haeckel writes in a recent letter that the total expense of establishing the museum will be about 200,000 M., of which 130,000 M. have so far been raised.

. . . .

In Germany there goes on a steady discussion of the *Vitalismus versus Mechanismus* subject. There is a constant running disputational conflict between the mechanicalists and the neo-vitalists. The latter find their champion in Hans Driesch, while among the former Otto zur Strassen is one of the most active: If Driesch were not so keen in his criticisms and so adroit in his argumentation victory would have been long ago with his antagonists, for he supports an impossible position. But he uses the method of offense and not of defense; he attacks the weak places in mechanicalism and constantly shifts the burden of proof to the shoulders of the mechanicalists. It is the method made famous, and for long successful, by Weismann, in his war on neo-Lamarckism. But Weismann had in the end, when his position was attacked, to make great concessions, and so it will be with Driesch. Neo-vitalism is really not new, despite its new terminology, but is simply paleo-vitalism very adroitly rehabilitated; and vitalism under any form is irreconcilable with the spirit of scientific progress.

A very interesting example of the advance of mechanicalism at the expense of vitalism on one hand and finalism on the other,

is that of the attitude and work of Dr Pierre Janet, the brilliant Salpetriere student of nervous functions. In a recent book, "Les Nevroses," and more especially in a course of lectures now being given in the Collège de France on the expression and influences of the emotions and sentiments, Janet discards almost entirely the finalistic explanations so well established by Darwin's epoch-making book. In their place he substitutes mechanistic explanations, and his reasoning has great cogency. The finalistic type of explanation of vital phenomena is very plausible and seizing. We snarl when we are angry because we want to scare our neighbor by showing him we are about to bite; or rather, as we no longer bite, we do it because our ancestors did when they wanted to warn their neighbors to keep to their own tree; and we smile because it is useful to show an opposite state of feeling.

But Janet—and others—find that smiling is the mechanically produced contortion of muscular stimulus due to strong emotional shock or mental agitation, and this mental agitation is not at all necessarily one of joy or friendliness or risibility. We smile often when we want to weep, when we are surprised, when we are embarrassed, when we are terrified. The facial muscles are roughly divisible into two unequal sets; one, above, of more and stronger muscles; the other, below, of fewer and weaker ones. When the stimulus comes the muscular pull of the upper set is stronger and our mouth corners go up and the contortion we call a smile is produced. But various emotions may produce the stimulus. If the contortion, that is the smile, is useful, well and good; but it is not a result of usefulness.

A brick is red because it contains by very virtue of being a brick certain chemical components in physical state, of which an attribute is redness. We ask for no further explanation of the brick's color. But let a butterfly's wing be red, and though the waste uric granules in its cuticular scales be of chemical and physical nature to compel them to absorb other colors and reflect red just as brick stuff does, we demand more explaining. We must have utility in this red; we must have a finalistic explanation, and if this explanation be not readily afforded by Darwinian selection or Lamarckian adaptation we have still left the ever-ready and always sufficient explanation of vitalism. The butterfly's wing is usefully red because the butterfly is alive.

We must admire the durability of the good old inheritance of acquired characters problem, even if its repeated resuscitation is sometimes a little less than interesting to us. However, our lessening of interest in it in no way reflects any lessening of its importance. It is still the *crux* of the whole species-forming problem. Neither mutations-theory nor Mendelism make its solution any less imperatively needed.

A recent important contribution, not of discussion alone but of new facts, to the inheritance of acquired characters problem is that of Jennings, who finds that, contrary to the admission on theoretical basis of even some of the most thoroughgoing anti-Lamarckians, acquired characters are not inherited in the Protozoa; at least in those Protozoa which were the subjects of Jennings's brilliant observation and experimentation. This may be a serious blow to the neo-Lamarckian side of the case—or it may not. It is if the old statement of the problem is to be always adhered to, but for some time now this statement has been recognized to be faulty and outworn. The neo-Lamarckian, taking the aggressive, prefers to put it this way: How are we to explain the fact that heritable differences distinguishing species or constant varieties (elementary species?) are often identical with those differences, uninherited, which can be produced ontogenetically among individuals of a single species of the group by submitting them to varying environmental or nutritional conditions? The fact exists and the presumption that it raises is that these identical species (heritable) differences have had the same ultimate causes which under our very eyes produce the non-heritable differences of the ontogenic varieties.

What is needed is the mechanism of cumulation or conversion of the non-heritable differences into identical heritable ones. This mechanism must, of course, concern itself with reproduction, with the germ-cells; and put as Jennings strongly puts it, it seems at first sight as if it must be an impossibly complex mechanism. But after all it is the change that has to be complex. The mechanism needed is one capable of producing changes of seeming great complexity. But comparatively simple mechanical transformers that produce very complex physiological changes are not unknown in biology, and there may, after all, be one awaiting discovery by Jennings, or some other

equally ingenious and persistent student of this good old enduring problem of acquired characters.

V. L. K.

PARIS, March, 1909.

DE VRIES'S SPECIES AND VARIETIES

Species and Varieties.—About two years ago De Vries's "Species and Varieties: their Origin by Mutation" was translated into German. A translation[1] of the same work has now appeared in French and no doubt it will ere long find a place in the literature of a number of other tongues.

As the first book which presented in a popular form the distinction between fluctuations and mutations, the world-wide circulation of this book means much for the advancement of modern biological conceptions. This is particularly true because a just delimitation of these two kinds of variations has been made, and can be made, only through the application of experimental methods. The result of the enlarged circulation of this work must be to stimulate the use of these methods among the biologists of every country in which it is made accessible.

The French edition was translated by Dr. L. Blaringhem, who is already well known because of his numerous studies on variations apparently induced by traumatism. He was a student of the well-known French biologist, the late Professor A. Giard, and to the memory of the latter, the French edition is dedicated. Professor Giard was to have written a preface to this edition, but illness which later resulted in his death rendered this impossible. A very brief prefatory note by the translator and one by the author are the only additions to the text of the English edition.

Already some subjects considered in this book could advangeously receive a somewhat different treatment, but it is perhaps better to allow the book to stand as it was originally written, so to take its position as a classic, retaining a historical value when its current biological value shall have been eclipsed by other works presenting the results of subsequent experimentation. This is evidently the attitude assumed by the author and

[1] De Vries, H. "Espèces et variétés: leur naissance par Mutation," *Traduit de l'Anglais par L. Blaringhem*, pp. viii + 548, 1909. Paris: Felix Alcan.

translator, in presenting this edition without amendment of any kind.

GEORGE H. SHULL.

EMBRYOLOGY

On the Totipotence of the First Two Blastomeres of the Frog's Egg.—It was found by Roux that if one of the first two blastomeres of the frog's egg is injured with a hot needle, the uninjured blastomere will develop into a *half* embryo. Morgan found, however, that if the egg were kept in an inverted position after the injury of one blastomere, the other would develop into a *whole* embryo. He attributes this difference to the rearrangement of the "mosaic" structure of the egg by flowing of substance, of different specific gravity (Born). However, he suggested to me that the half embryo obtained by Roux might be due to the presence of the injured blastomere. In Triton, when the first two blastomeres are separated, each gives rise to a whole embryo (in case the first cleavage plane would have become the median plane). I have been trying various methods for removing one of the first two blastomeres of the frog's egg, and succeeded in getting a small per cent. of the remaining blastomeres (of *Chorophilus triseriatus*) to develop. The puncture of the egg membrane caused it to shrink down on the remaining blastomere and left an opening for bacteria. Although there was a great mortality in the operated eggs, quite a number of them gastrulated (*as wholes*), and several of them reached the tadpole stage. The pressure of the egg membrane seemed to hinder their further development and none of them hatched, although one lived until I fixed it for sectioning, after the control eggs had hatched. In no case was a half gastrula found, and as this is the earliest stage at which the bilateral symmetry is very pronounced, *all of the embryos were wholes as far as could be observed.* Probably all operated eggs in which the median plane would not have coincided with the first cleavage plane died before gastrulation.

J. F. MCCLENDON.

UNIVERSITY OF MISSOURI, April 8, 1909.